REVUE SUISSE DE ZOOLOGIE. vol. hors série: 203-210; août 1996

How do crab spiders (Thomisidae) bite their prey ?

Rainer F. FOELIX
Aargauisches Naturmuseum. Feerstr. 17, CH-5000 Aarau, Switzerland.

How do crab spiders (Thomisidae) bite their prey? - Preying crab spiders (*Xysticus, Diaea*) are typically pictured as holding their victims in a neck grip. A closer inspection shows that the initial bite can occur anywhere. After the prey is immobilized, the bite site may be changed to the "neck" - more precisely the back of the head. Other parts of the prey's body (thorax, abdomen, legs) are also bitten and fed upon. Feeding lasts many hours and is achieved solely through the tiny bite holes, leaving a completely intact carcass. The actual bite holes are difficult to see because they are usually clogged by dried-up hemolymph; however, by using a scanning electron microscope, they could be made visible on discarded flies. It is inferred that the cheliceral fangs are partially withdrawn during feeding to allow extra-oral digestion.

Key-words: crab spiders - prey capture - chelicerae - bite marks - feeding

INTRODUCTION

Crab spiders are well-known as ambush predators, sitting camouflaged on flowers. Insects visiting these flowers are grasped with the strong front legs and immediately bitten. It seems that the spider typically performs a "neck bite"- at least, that is what we find written or illustrated in most spider text books (BRISTOWE 1941, 1971; FOELIX 1992; MAIN 1976). However, there are only few observations on the initial attack, i.e. whether the crab spider aims immediately toward the neck, or whether the first bite may also occur on other parts of the victim's body (Lubin, 1983; POLLARD 1990, 1993; K.S. ERICKSON & D.H. MORSE, pers. comm.). Also, what exactly is meant by "neck" in an insect? Is the primary target the soft intersegmental membrane rather than any solid cuticle of the head or thorax?

Crab spiders are also renowned for leaving an almost intact yet empty shell after feeding on a prey. Apparently they just "suck out" their victims through the tiny bite holes (HOMANN 1934, 1975). It is difficult to imagine how this can be achieved effectively, - especially since the bite holes are supposedly plugged by the cheliceral fangs.

Manuscript accepted 22.01.1996.
Proceedings of the XIIIth International Congress of Arachnology, Geneva, 3-8.IX.1995.

The purpose of this brief study was thus two-fold: (1) to determine the exact location of crab spider bites on their prey, and (2) to find out how digestion could take place in a seemingly unharmed prey.

MATERIALS AND METHODS

Subadult and adult female crab spiders (*Xysticus cristatus* Clerck, 1757; *Diaea dorsata* Fabricius, 1777) were kept in small, clear plastic containers with moist blotting paper on the bottom. Dipteran flies were used as prey: for *Xysticus* rather large varieties such as house flies and flesh flies, for *Diaea* smaller varieties (such as syrphids) or stunned house flies. Prey capture was observed under a binocular microscope and close protocols were kept for each capture, at least during the first hours (some spiders kept feeding on large prey over night - for up to 24 hours!). When the spider had finished feeding, the fly carcass was removed and either air-dried or kept in alcohol and later dried with the critical point method. After sputtering with gold the specimens were mounted and oriented on carbon-coated stubs and inspected in a scanning electron microscope (Cambridge Scientific) at magnifications from 20 - 2'000 x.

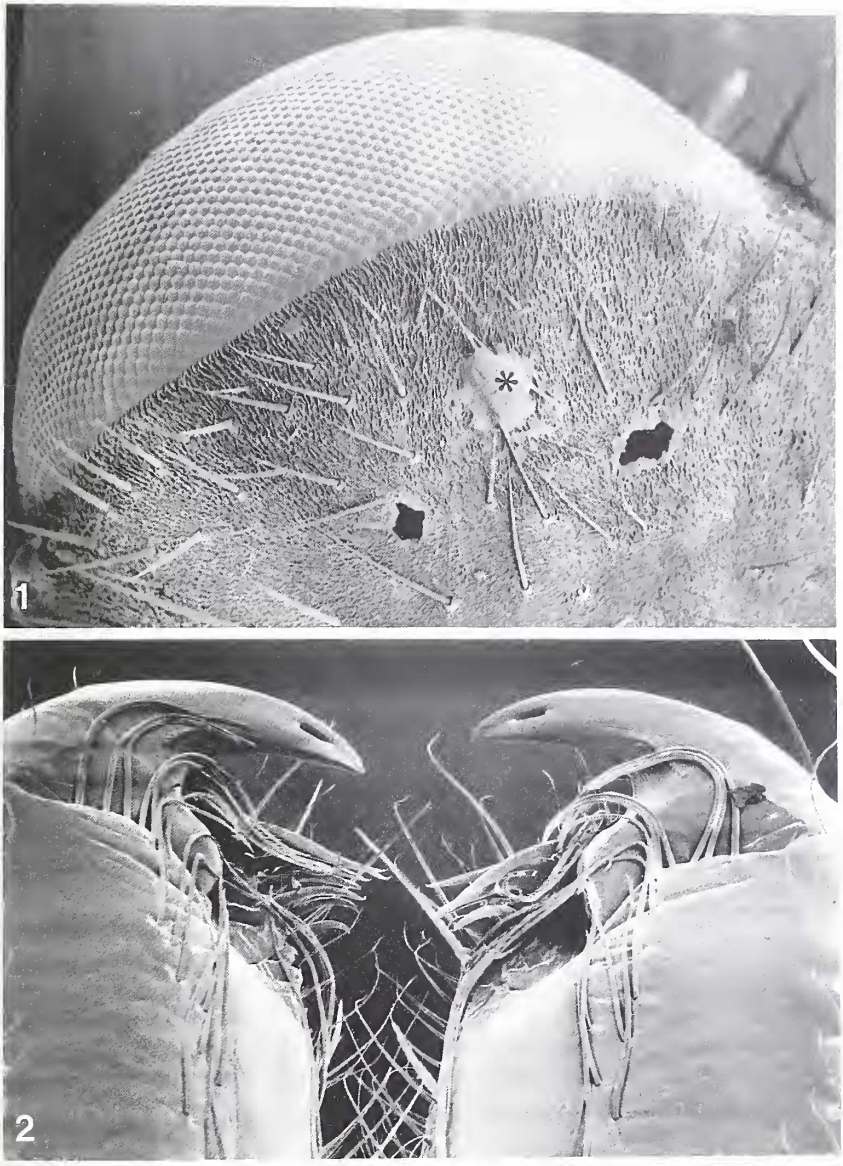
RESULTS

Bites and bite marks

Although it is easy to watch a crab spider feeding on a prey, it is much more difficult to witness the initial attack - even under experimental conditions. From several observations, mainly on *Xysticus*, I can state that the very first bite does not necessarily occur in the "neck" region but may happen at other regions of the prey's body as well.

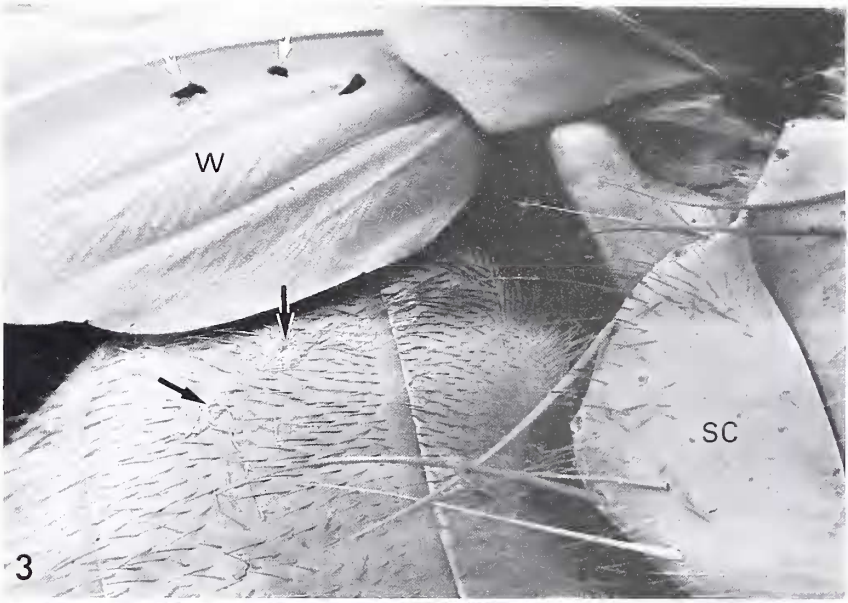
During the first (evenomating) bite the chelicerae are widely spread (up to 90°) and the fangs are buried into the prey. The strong front legs are only initially used to hold the prey but are soon withdrawn and only the palps and chelicerae are kept in contact. Caught flies may buzz heavily at first but become motionless within 3-4 minutes. After about 10 minutes the spider usually releases both chelicerae and may apply a second bite - usually in the head region. Now, however, the basal segments of the chelicerae are no longer spread but kept nearly parallel. Presumably this bite will not use any further venom but serves just to hold the prey in place before feeding begins.

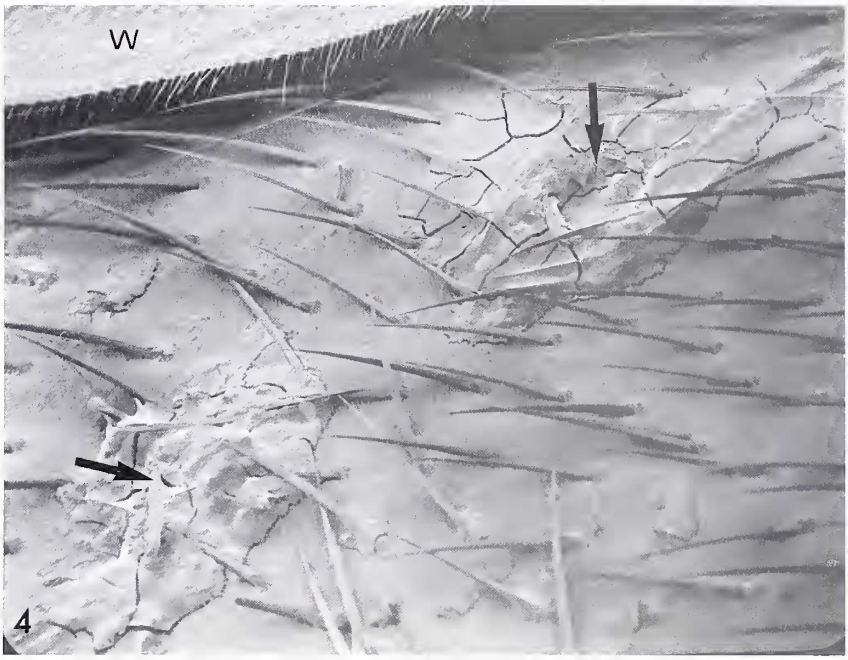
If the famous "neck grip" is inspected more closely, it can be seen that the cheliceral fangs usually pierce the back of the head but not the soft membrane ("neck") connecting head and thorax (Fig. 1). The compound eyes are also often a target and they are the only spot where the bite marks can be seen clearly afterwards. The bite holes are necessarily small because they correspond roughly to the diameter of the cheliceral fangs (Fig. 2). They usually become clogged with dried-up hemolymph (or digestive fluid of the spider) and this makes it difficult to detect them (Figs 3, 4).



FIGS 1-2

Fig. 1. Backside of fly's head showing two bite holes from a *Xysticus cristatus*. The bite marks lie closely together (320 μm), which indicates that they did not result from the first evenomating bite but were made later for the purpose of feeding. Some remnants from feeding are indicated by the asterisk. 110 x. Fig. 2. The cheliceral fangs (rear view) that inflicted the bite holes seen in Fig. 1. Note the distinct openings of the poison canals and the lack of cheliceral teeth. 165 x.





FIGS 3-4

Fig. 3. Dorsal view of a blowfly carcass after a *Xysticus* had fed on it. The cheliceral fangs had first punctured the left wing (W, white arrows) and were then pushed into an abdominal segment. The actual bite holes (black arrows) are almost obscured by dried-up hemolymph and digestive juice. *Sc, scutellum*. 55 x. Fig. 4. Higher magnification of the abdominal bite holes (arrows) indicated in Fig. 3. 240 x.

Other sites that may be bitten include the thorax, the abdomen and the legs. Again, it is noteworthy that the spider does not seek out any particular soft parts such as joints or intersegmental membranes. The chelicerae are apparently not as weak as generally believed (e.g. GERTSCH 1949) and can easily penetrate the tegmata of the abdomen (see Fig. 3) or the solid cuticle of the legs (Fig 5).

Even if a fly is initially bitten into the distal abdomen, it will become quickly paralyzed (within 3-4 minutes). This is surprising because it is commonly implied that bites into the head or thorax are advantageous because the venom would act directly at the near-by central nervous system. POLLARD (1990) claims that a second bite in the head region would inject further venom and thus cause paralysis. However, this may not be necessary since I observed *Xysticus* changing after 10 minutes from the abdomen to a leg, while the fly was already completely immobile. On the other hand, I also noted some incomplete paralysis: In one strange incident a fly, while being bitten into the thorax, responded by laying eggs in a coordinated fashion for several minutes; apparently the abdominal ganglia were not affected by the venom during that time.

Most authors agree that crab spiders must have a very potent venom since they subdue large prey (e.g. bumble bees) quite rapidly (MORSE 1979, 1981, 1983). Although this is a reasonable assumption, no real physiological data on the toxicity of thomisid poison are available to date.

FIG. 5

Relatively large bite marks (200 µm long) on the femur of a fly's leg, due to a *Xysticus* that had been feeding on it. Dried-up hemolymph (*) is visible on the leg surface. 120 x.

Feeding

It is well-known that the prey of crab spiders is not chewed up during feeding but is apparently sucked out through the bite holes so that an almost intact but empty shell remains. The question then arises how any fluid could be extracted from the prey since even the tiny bite holes are supposedly plugged by the cheliceral fangs. I had noticed that during feeding the basal segments of the chelicerae are no longer spread apart but kept parallel. Although I could not see it directly under the microscope, I assumed that the cheliceral fangs might be withdrawn from the bite holes to allow an exchange of fluid during feeding. However, the fact that a prey is attached firmly (and only) to the chelicerae, even when the spider is sitting on a vertical wall with its head down, contradicts this assumption. Perhaps the cheliceral fangs are slightly withdrawn from the bite holes, thereby opening a small space for fluid exchange.

During feeding some digestive fluid appears around the mouth parts of the spider for several seconds, and is then sucked back. This alternating flow could also be followed inside the prey, for instance when air bubbles were present inside a fly's leg. Air is apparently drawn into the prey through the bite holes when the spider stops suction and releases digestive fluid. When discarded flies where dissected under water, there were always "large" air bubbles present, indicating that the sucked out body juices had been replaced by air. Considering that the bite holes are very small and at least partly plugged by the cheliceral fangs, it is not surprising that crab spiders feed for many hours on one prey item. They certainly change their feeding location several times on one prey, often staying for an hour or more at one particular spot. I did not notice clearly preferred areas nor a specific sequence in the feeding locations.

Whether a prey is consumed completely or only partially, may depend on several factors. Obviously, if a prey is very large, the spider may be saturated after having taken in only part of it. For instance, I dissected fly carcasses in which the head and thorax were empty, whereas the abdomen appeared internally unchanged; in other cases the flight muscles inside the thorax were practically unaffected. After a long feeding time the spider's abdomen becomes visibly enlarged, indicating that a substantial part of the prey has been taken in. I did not attempt to measure the actual gain in weight since detailed measurements were recently performed on crab spiders by Erickson & Morse (in prep.).

DISCUSSION

The starting point for this small study was the question whether crab spiders always and exclusively apply the "neck bite" when attacking their prey. It turned out that the first bite may actually occur anywhere on the prey's body. After a few minutes the prey becomes immobile and then the spider will start feeding on it. This will often - but not always - be in the head region. The actual bite marks lie usually on the back side of the head ("neck") or in the compound eyes. Feeding may also commence on the legs, the thorax or the abdomen, at least in the two species observed here (*Xysticus cristatus*, *Diaea dorsata*). This differs somewhat from the pattern seen in a New Zealand *Diaea* species, which initially attacks the head or thorax and also starts feeding

there, before changing to the abdomen (POLLARD 1990). In another thomisid (*Misumena vatia*) the initial strikes were found to be at almost random sites, though mostly in the head (Erickson & Morse, pers. comm.). Whether the fly's head is actually recognized during the first attack is unclear. It is remarkable, however, that *Diaea* sp. re-orients quickly toward a fly's head, if she had first bitten into the thorax or abdomen (POLLARD 1990). This was shown quite convincingly by artificially attaching a fly's head to a larva: as soon as the spider touched this head with the front tarsi, she would change the bite site to the head. A definite order of preference for the various body parts of a fly was also ascribed to the predatory behaviour of *Philodromus* (formerly Thomisidae) by HAYNES & SISOJEVIC (1966). The sequence would start with the eyes and head, followed by the thorax and abdomen and would end with the legs. In *Xysticus cristatus* and *Diaea dorsata* I could not find such an order of preference. The fact that the head is bitten more often is probably simply a consequence of an insect landing "head-on" on a flower and thus practically facing a waiting crab spider.

The puzzling question how a crab spider could extract any fluid from its prey through the tiny bite holes - which are furthermore clogged by the cheliceral fangs - has been addressed in more detail by POLLARD (1990). He noted that the chelicerae are inserted differently into the prey during the feeding process, and that the cheliceral fangs are apparently turned horizontally, thus holding the prey in a fixed position. This corresponds closely to my own observations on *Xysticus* and *Diaea*. I also follow his argument that the spider's digestive fluid can enter the prey's body when the cheliceral fangs are partially or totally retracted from the bite hole when the sucking stops (relaxation phase). In any case, there is always a regular alternation between sucking and relaxing that ensures an exchange of fluid between the spider and its prey. During the sucking phase the spider should be able to make a tight seal with its mouth parts around the bite holes in order to create a pressure deficit in the prey. Given the anatomy of the mouth parts (labium, maxillae, chelicerae) it is difficult to imagine how this could be achieved. These details in the feeding mechanism of crab spiders certainly deserve further study.

It is generally stated that spiders equipped with cheliceral teeth mash up their prey into an unrecognizable mass whereas spiders lacking such teeth inflict only small bite holes but otherwise leave their prey intact (BRISTOWE 1941, 1971; FOELIX 1992). Crab spiders certainly belong to the latter category (Fig. 2). This general rule stated above is probably more a rule-of-thumb, since there are many exceptions. For instance, some spiders that have cheliceral teeth still leave their prey almost intact, e.g. *Linyphia* (TURNBULL 1960) or *Stegodyphus* (own unpubl. observ.). Chewing up a prey and soaking it in digestive fluid would seem the physiologically more efficient method. Why some spiders (thomisids, theridiids, mimetids) prefer the more time-consuming sucking method still needs to be elucidated.

ACKNOWLEDGEMENTS

I thank Douglass Morse, Kristin Erickson, Yael Lubin, Simon Pollard and Jerome Rovner for sharing their knowledge of crab spiders with me, and Peter Kaufmann for collaboration on the scanning electron microscope.

REFERENCES

BRISTOWE, W.S. 1941. The Comity of Spiders. *Ray Society London*, No. 128: 1 - 560.

BRISTOWE, W.S. 1971. The World of Spiders. *Collins, London*: 1 - 304.

FOELIX, R.F. 1992. Biologie der Spinnen. *Thieme, Stuttgart*: 1 - 331.

GERTSCH, W.J. 1949. American Spiders. *Van Nostrand, New York*: 1 - 285.

HAYNES, D.L. & SISOJEVIC, P. 1966. Predatory behavior of *Philodromus rufus* Walckenaer (Araneae: Thomisidae). *The Canadian Entomologist* 98: 113 - 133.

HOMANN, H. 1934. Beiträge zur Physiologie der Spinnenaugen. IV. Das Sehvermögen der Thomisiden. *Zeitschrift für vergleichende Physiologie* 20: 420 - 429.

HOMANN, H. 1975. Die Stellung der Thomisidae und der Philodromidae im System der Araneae (Chelicerata, Arachnida). *Zeitschrift für Morphologie der Tiere* 80: 181 - 202.

LUBIN, Y.D. 1983. An ant-eating crab spider from the Galapagos. *Noticias de Galapagos* 37: 18 - 19.

MAIN, B.Y. 1976. Spiders. *Collins, Sydney*: 1 - 296.

MORSE, D.H. 1979. Prey capture by the crab spider *Misumena calycina* (Araneae: Thomisidae). *Oecologia, Berlin*, 39: 309 - 319.

MORSE, D.H. 1981. Prey capture by the crab spider *Misumena vatia* (Clerck) (Thomisidae) on three common native flowers. *The American Midland Naturalist* 105: 358 - 367.

MORSE, D.H. 1983. Foraging patterns and time budgets of the crab spiders *Xysticus emertoni* Keyserling and *Misumena vatia* (Clerck)(Araneae: Thomisidae) on flowers. *The Journal of Arachnology* 11: 87 - 94.

POLLARD, S.D. 1990. The feeding strategy of a crab spider, *Diaea* sp. indet. (Araneae: Thomisidae): post-capture decision rules. *Journal of Zoology, London*, 222: 601 - 615.

POLLARD, S.D. 1993. Little murders. *Natural History* 102(10): 58 - 65.

TURNBULL, A.L. 1960: The prey of the spider *Linyphia triangularis* (Clerck) (Araneae, Linyphiidae). *Canadian Journal of Zoology* 38: 859 - 873.